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Size and Scaling in the Indian Frogs *Nyctibatrachus* and *Nannobatrachus* (Ranidae)

H. Bradley Shaffer

A Contribution in Celebration
of the Distinguished Scholarship of Robert F. Inger
on the Occasion of His Sixty-Fifth Birthday

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- CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif., 943 pp.
- GRUBB, P. J., J. R. LLOYD, AND T. D. PENNINGTON. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. *Journal of Ecology*, 51: 567-601.
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- MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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Size and Scaling in the Indian Frogs *Nyctibatrachus* and *Nannobatrachus* (Ranidae)

Abstract

The Indian ranid genera *Nannobatrachus* and *Nyctibatrachus* have traditionally been differentiated primarily on the basis of size: *Nannobatrachus* is extremely small, while *Nyctibatrachus* ranges from medium to large. Recently described species of *Nyctibatrachus*, however, have eliminated this size gap and call the validity of *Nannobatrachus* into question. Bivariate and multivariate analyses of eight morphometric variables were used to describe the patterns of size-related scaling within *Nyctibatrachus* and to compare it to the tiny *Nannobatrachus beddomi*. Speciation among species of *Nyctibatrachus* appears to have occurred by shifting species means along a common series of allometric trajectories; species scale in the same way and vary primarily in adult size. *Nannobatrachus* follows exactly the same pattern and on morphometric criteria is virtually indistinguishable from adult *Nyctibatrachus minor* or juveniles of larger species. On the basis of these morphometric data, it appears that generic distinction of *Nannobatrachus* is not justified.

Introduction

The Western Ghats of southern India are known for their diverse and unique fauna, and the phylogeny and biogeography of this area have long been of interest to students of animal distribution and systematics (Hora, 1953). The anuran fauna

of the Western Ghats is no exception, with several very distinctive genera and species limited to the mountains of south India and Sri Lanka. Among the most unusual are the ranid frog genera *Nyctibatrachus* and *Nannobatrachus*.

Both genera were described by Boulenger (1882): *Nyctibatrachus* currently contains seven species (Pillai, 1978; Inger et al., 1984), while *Nannobatrachus* consists of a single diminutive form (Inger et al., 1984). Aside from the apparent close relationships of these two genera to each other and to *Nannophrys* from Sri Lanka (Boulenger, 1882; Clarke, 1983), very little is known of their phylogenetic relationships. Noble (1931) placed all three in the subfamily Raninae, recognizing only the shape of the pupil and the degree of ossification of the osmosternum as diagnostic characters. Noble was not convinced of the distinctiveness of these genera and felt that "it is a matter of opinion whether these can be considered valid generic differences" (Noble, 1931, p. 519). While Clarke (1983) presents convincing evidence that *Nannophrys* is distinct, his analysis also emphasizes the close relationship between *Nannobatrachus* and *Nyctibatrachus*.

Size reduction has been a key factor in the evolutionary radiation of these frogs. *Nannobatrachus* consists solely of the tiny *Na. beddomi* (mean snout-vent length [SVL] = 15 mm), while *Nyctibatrachus* spans a size range from the small *N. pygmaeus* (mean SVL = 20 mm) to *N. major* (mean SVL = 45

mm) (Boulenger, 1882; Inger et al., 1984). This size variation has two potentially important consequences. First, it has been cited as an important systematic character at the species and generic levels (e.g., Myers, 1942; Clarke, 1983). Second, it suggests that size-related scaling may be an important mode of morphological evolution in these frogs.

During recent fieldwork in the Western Ghats with Robert F. Inger, two new species of *Nyctibatrachus* were discovered which bridge the size gaps between these two genera and between the large and small species of *Nyctibatrachus*. *Nyctibatrachus minor* is a very small species (15–21 mm SVL; Inger et al., 1984), and is directly comparable in size with *Na. beddomi*. *Nyctibatrachus aliciae* is a medium-sized species (20–33 mm SVL; Inger et al., 1984) and forms a link between the diminutive *N. minor* and *N. pygmaeus* and the larger *N. major*. In addition, since four of these species (*N. aliciae*, *N. major*, *N. minor*, and *Na. beddomi*) were collected in microsympatry (Inger et al., 1984), comparisons among taxa are not confounded by problems of geographic variation.

Here, I use bivariate and multivariate morphometric analyses to explore patterns of variation within and among species of *Nyctibatrachus* and *Nannobatrachus*. I use these analyses to focus on two major questions: (1) Are patterns of size-scaling among species generally extensions of similar patterns found within species, or has the evolutionary diversification of these frogs along a size axis involved additional shape differentiation? (2) Is the recognition of *Nannobatrachus* justified on morphometric grounds, or does it appear to be simply an extension of the general size-related trends found within *Nyctibatrachus*? This second point is especially important, since the absolute size gap separating the two genera no longer exists, weakening previous arguments that *Nannobatrachus* is a justifiable genus on the basis of size alone.

Materials and Methods

Specimens and Morphometric Variables

All specimens of *Nyctibatrachus aliciae*, *N. major*, and *N. minor* and *Nannobatrachus beddomi* were collected in the vicinity of Ponmudi, Kerala State, India, between 3 May and 17 June 1982 as part of a joint project of the National Museum of Natural History, New Delhi, and Field Museum of Natural History, Chicago. The collection was

made near the Ponmudi ridge (08°45'N, 77°08'E) between 110 and 940 m altitude. Frogs were collected along or in small forest streams or under cover objects, near seeps or low, wet areas (see Inger et al., 1984, for additional ecological information). For comparative purposes, I examined specimens of *N. humayuni* and *N. pygmaeus* from the British Museum (Natural History).

All Field Museum specimens were preserved within four hours of capture in buffered formalin and later transferred to 95% ethanol. The following Field Museum of Natural History (FMNH) and British Museum (Natural History) (BMNH) specimens were measured for this study: *N. aliciae*—FMNH 216582–216600, N = 19 (9 females, 8 males, 2 immatures); *N. humayuni*—BMNH 1958.1.4.24, 1958.1.4.27, N = 2 (both female); *N. major*—FMNH 218198–218288, N = 91 (13 females, 18 males, 60 immatures); *N. minor*—FMNH 216603–216605, 216607–216618, N = 15 (2 females, 9 males, 4 immatures); *N. pygmaeus*—BMNH 1947.2 + 45, 1947.2 + 48, 1947.2 + 54, N = 3 (all female); *Na. beddomi*—FMNH 218088–218098, N = 11 (6 females, 4 males, 1 immature). Sexual maturity was determined by the presence of femoral glands in males and pigmented ova or convoluted oviducts in females.

Nine external measurements were recorded for each preserved specimen: snout-vent length, from the tip of the snout to the posterior edge of the body (SVL); head width, measured at the angle of the jaw (HWJ); distance between the eyes at the medial edge of the eye (INTORB); distance between the nostrils (INTNAS); head length, from the tip of the snout to the posterior margin of the mouth (HEADLEN); distance from the vent to the knee joint (FEMUR); distance from the knee to the ankle joint (TIBIA); distance from the ankle joint to the tip of the fourth (longest) toe (HINDFOOT); and distance from the elbow to the tip of the third (longest) finger (FORELIMB). Bilateral characters (HEADLEN, FEMUR, TIBIA, HINDFOOT, FORELIMB) were measured on the right side of the specimen, unless a limb was obviously distorted or injured, in which case the left side was used. All measurements were taken to the nearest 0.1 mm, either with a Helios dial caliper or a Wild dissecting microscope ocular micrometer. These measurements were chosen in an attempt to document the general size and shape of the animal while avoiding variance introduced by nutritional state or the presence of eggs. The nontraditional marker of the edge of the mouth for head length was chosen because no other landmark could be reliably located.

Statistical Analysis

I used SVL as a single variable indicator of body size in both bivariate and multivariate analyses. While other methods of quantifying size and shape variation exist, I used this approach both for ease of interpretation and to avoid the problems involved in confounding size and shape variation in principal component approaches (Humphries et al., 1981). In bivariate scaling analyses, all variables were plotted against SVL as a common size factor. In multivariate analyses, I used residuals from bivariate regressions of each variable against SVL to construct a vector of size-independent measurements for each specimen (RHWJ, RINTORB, etc.; see Radinsky, 1981; Shaffer, 1983, 1984, for similar applications).

In bivariate analyses, regression statistics, including confidence limits, were calculated *only* for *N. aliciae*, *N. major*, and *N. minor*, since they were all collected by us from the same region, and are all clearly assignable to a single genus. Measurements for *N. pygmaeus*, *N. humayuni*, and *Na. beddomi* were then plotted on these graphs and examined for goodness of fit. To construct simultaneous confidence intervals (CI) for all predicted values, I used the standard error of prediction (SE-PRED; Weisberg, 1980, p. 21)

$$\text{SEPRED}(y|x) = \sigma[1 + (1/n) + (x - \bar{x})^2/\text{SXX}]^{1/2} \quad (1)$$

where σ is the square root of the residual mean square in the analysis of variance, n is the sample size, x is the value of SVL being analyzed, \bar{x} is the mean SVL, and SXX is the corrected sum of squares of x . This value is called the standard error of the residual in the SAS regression procedure (SAS, 1982) which was used to calculate it. To calculate simultaneous CI for all possible predicted values, I followed Weisberg (1980) in using

$$[2F(\alpha; 2, n - 2)]^{1/2} \quad (2)$$

as a multiplier instead of the normal multiplier from the t distribution. This results in wider, less constricted CI than those in the normal SAS analysis, but provides intervals more consistent with the alpha values ($P < .05$ was used in all cases).

In multivariate analysis, regressions were recalculated using all species, and residuals from these lines were used for each specimen. These size-independent measurements were then subjected to a series of discriminant function analyses to quan-

tify shape differences among the six species. To evaluate the contribution of individual variables to the discriminant functions, I used the total canonical structure coefficients (Klecka, 1980). These coefficients are simply the product-moment correlations between an observation's discriminant function score and its value for each variable. Klecka (1980) discusses the virtues of this over the more traditionally used standardized canonical coefficients.

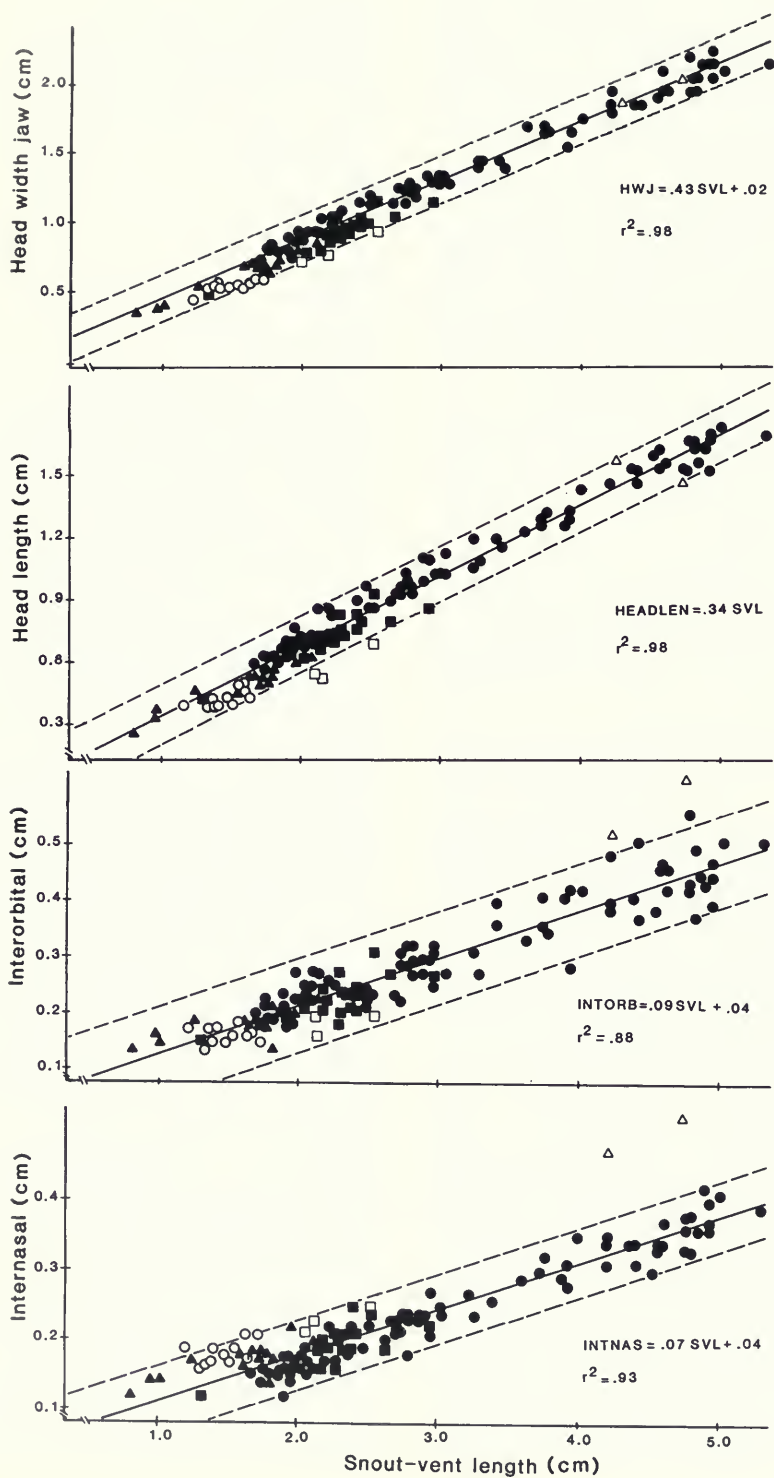
Results

Bivariate Analyses

Scatter plots, regression lines, and CI for predicted values for all eight characters against SVL are provided in Figure 1. (Equations (1) and (2) produce CI which lack the constriction at the bivariate mean normally found for confidence limits for the slope of a regression line.) Since regression equations and CI were calculated only for *Nyctibatrachus aliciae*, *N. major*, and *N. minor*, these lines may be used to test independently how well the remaining species conform to the expectations generated from these species. Because all relationships are linear and residuals are not correlated with SVL, no transformations of the data were necessary.

In general, *Nannobatrachus beddomi*, *N. humayuni*, and *N. pygmaeus* conform remarkably well to the general size relationships derived from the other *Nyctibatrachus* species. These results are summarized in Table 1, which lists for each character both the number of individuals that fall outside the 95% CI for predicted values and the number of individuals falling above or below the regression line. Individuals outside the CI show a strong deviation from expectations derived from regression. However, if the regression truly describes the bivariate relationship between two variables, then observations should be equally distributed above or below the line. Thus, mild non-conformity of observations to the regression line may lead to all observations falling within the CI but above or below the line.

Nannobatrachus beddomi conforms well to the predicted regression lines. For five of eight variables, no observations fall outside the confidence limits, and only for INTNAS do a substantial number (four of 11) fall beyond the confidence limits. For five variables (HWJ, INTNAS, HEADLEN, FEMUR,



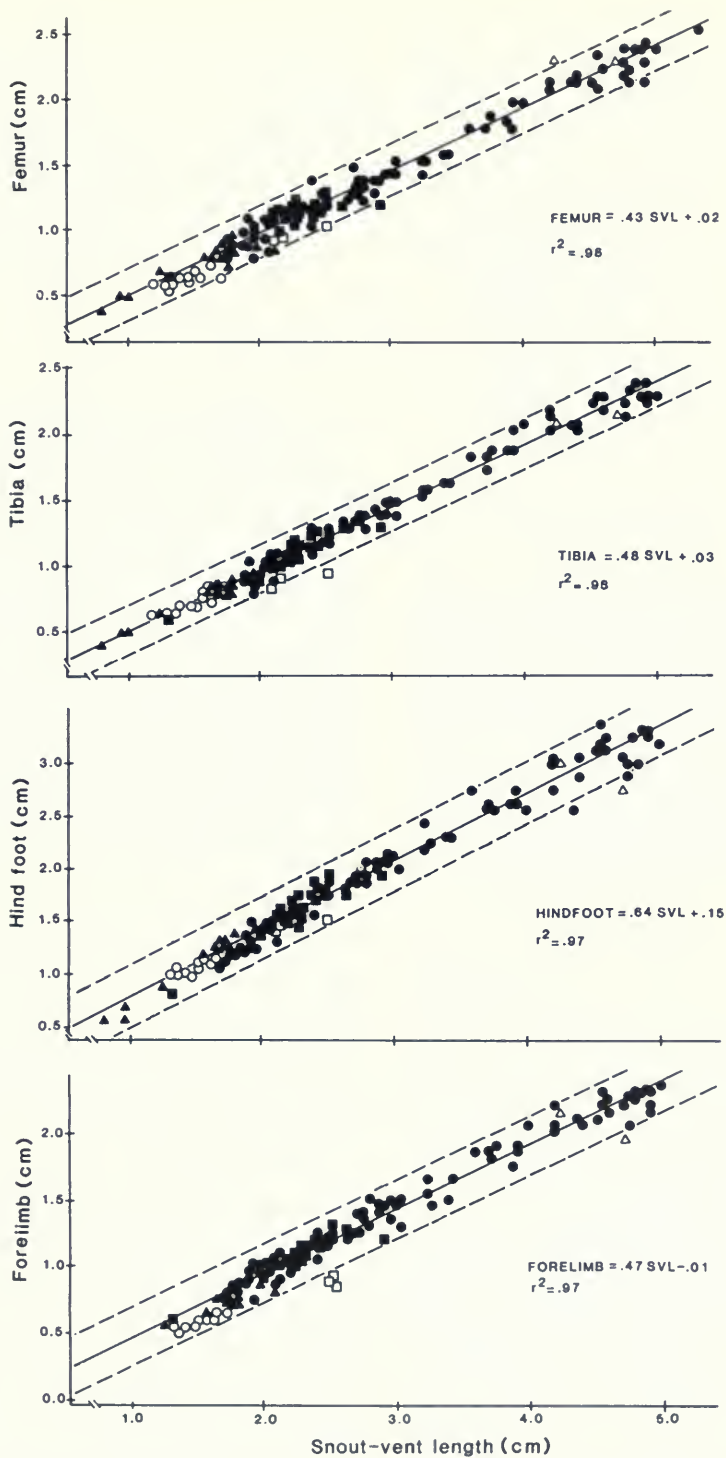


FIG. 1. Plots of eight morphometric variables (opposite page, HWJ, HEADLEN, INTORB, INTNAS; above, FEMUR, TIBIA, HINDFOOT, FORELIMB) against snout-vent length (= size). In all cases the least squares regression (solid line) and simultaneous 95% confidence limits for predicted values (dashed lines) were fit to the solid symbols only. ● = *Nyctibatrachus major*; ▲ = *N. minor*; ■ = *N. aliciae*; ○ = *Nannobatrachus beddomi*; △ = *N. humayuni*; □ = *N. pygmaeus*.

TABLE 1. Numbers of specimens out of the total examined falling outside 95% confidence intervals for predicted values, followed (in parentheses) by the number falling above (+) and below (–) the regression fitted to *Nyctibatrachus aliciae*, *N. major*, and *N. minor*.

Mea- sure- ment	<i>Na. beddomi</i>	<i>N.</i> <i>pygmaeus</i>	<i>N. humayuni</i>
HWJ	1/11 (11–)	1/3 (3–)	0/2 (2–)
INTORB	0/11 (4+, 7–)	0/3 (3–)	2/2 (2+)
INTNAS	4/11 (11+)	0/3 (3+)	2/2 (2+)
HEAD- LEN	0/11 (10–, 1+)	3/3 (3–)	1/2 (2–)
FEMUR	1/11 (10–, 1+)	1/3 (3–)	1/2 (1–, 1+)
TIBIA	0/11 (3+, 8–)	2/3 (3–)	0/2 (1+, 1–)
HIND- FOOT	0/10 (2+, 8–)	0/3 (3–)	1/2 (1+, 1–)
FORE- LIMB	0/9 (9–)	3/3 (3–)	1/2 (1+, 1–)

FORELIMB), virtually all individuals fall above or below their respective lines (table 1; fig. 1), indicating some lack of fit to expectations. However, in most cases this tendency is mirrored in *N. minor*, suggesting an allometric relationship associated with extremely small size (fig. 1).

Nyctibatrachus pygmaeus and *N. humayuni* both appear to show stronger deviations from the Ponnudi samples than do sympatric *Nannobatrachus*. Although sample sizes are extremely small (three

N. pygmaeus, two *N. humayuni*), most or all individuals fall outside CI for several variables in both species (table 1). Because of the limited samples available and the possible biases involved in the different durations and states of preservation of these specimens, the results must be interpreted cautiously. However, these data do suggest that *N. humayuni* and *N. pygmaeus* are distinctive taxa and that *Na. beddomi* is not particularly unique.

Multivariate Analysis

The discriminant function analysis produces linear combinations of the original variables (canonical variables or discriminant functions) that maximize the among-group component of variance. Since size-independent data were used, I can assess whether shape differences exist among samples of these six species. If they differ *only* in SVL, then species should be indistinguishable when using residuals from regressions on SVL. Because discriminant function analysis is an extremely powerful tool for differentiating groups (Klecka, 1980), the technique represents a strong test for among-taxon differences which must be interpreted with caution (e.g., Shaffer, 1984). However, if groups are similar, then this analysis strongly suggests that no shape differences exist in the eight variables examined.

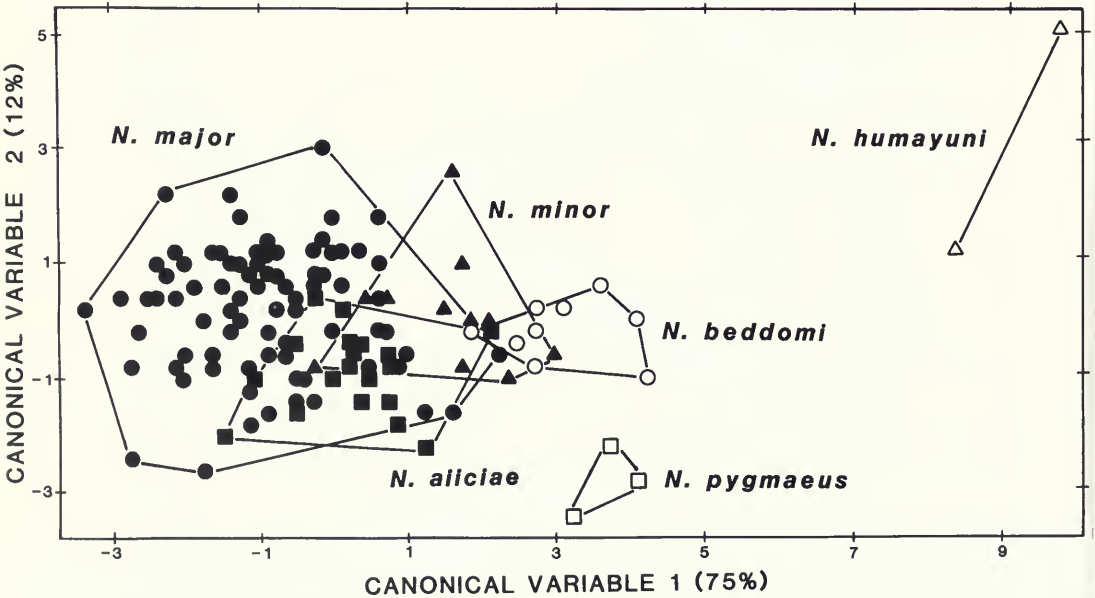


FIG. 2. Plot of all individuals having complete data on the first two canonical variables of a discriminant function analysis. Symbols as in Figure 1. Proportion of variance explained by each variable in parentheses.

TABLE 2. Classification matrix based on discriminant function analysis for all six species of *Nyctibatrachus* and *Nannobatrachus*.

Species	No. of observations and % classified into					
	<i>N. minor</i>	<i>N. aliciae</i>	<i>N. major</i>	<i>N. humayuni</i>	<i>Na. beddomi</i>	<i>N. pygmaeus</i>
<i>N. minor</i>	9 81.8	0 0.0	0 0.0	0 0.0	2 18.2	0 0.0
<i>N. aliciae</i>	0 0.0	17 89.4	1 5.3	0 0.0	1 5.3	0 0.0
<i>N. major</i>	4 4.5	17 19.1	66 74.2	0 0.0	0 0.0	2 2.2
<i>N. humayuni</i>	0 0.0	0 0.0	0 0.0	2 100.0	0 0.0	0 0.0
<i>Na. beddomi</i>	2 22.2	0 0.0	0 0.0	0 0.0	7 77.8	0 0.0
<i>N. pygmaeus</i>	0 0.0	0 0.0	0 0.0	0 0.0	0 0.0	3 100.0

A plot of all individuals on the first two canonical variables demonstrates high group overlap among *Nyctibatrachus aliciae*, *N. minor*, *N. major*, and *Nannobatrachus beddomi* (fig. 2). Together, the first two canonical variables account for 87% of the total variance in the data set, suggesting that they give a fair representation of the total pattern of multivariate dispersion. Only *N. pygmaeus* and *N. humayuni* stand apart as distinctive, further supporting their interpretation as morphologically distinct taxa.

Another way of viewing multivariate group overlap is from the outcome of a classification procedure where each individual's generalized distance to each group centroid is calculated, and observations are classified according to proximity to the nearest centroid (Fisher, 1936; Klecka, 1980). If group overlap is low, misclassifications will be rare. Because the inclusion of groups with very small numbers of observations can seriously bias these classifications, the analysis was performed with all six groups and with only the four largest; the resulting functions were then used to classify the remaining observations. Both gave concordant patterns, and I present only the results using all six groups (table 2). These results confirm the pattern shown in Figure 2; that is, some overlap exists between *N. minor* and *Na. beddomi*, *N. aliciae* and *N. major*, and to a lesser extent, between *N. aliciae* and *Na. beddomi*. The small samples of *N. humayuni* and *N. pygmaeus* were unambiguously classified into their respective species.

Total canonical structure coefficients for the first two canonical variables (CV) are provided in Table 3. The INTERNAS and HEADLEN are most highly correlated with CV-1, and as such are most im-

portant in differentiating *Na. beddomi*, *N. pygmaeus*, and *N. humayuni* from the remaining taxa. The HWJ and INTORB correlate most strongly with CV-2, and are thus particularly important in distinguishing *N. humayuni* and *N. pygmaeus* from the remaining groups (see fig. 2). It is important to note that the correlations between INTNAS and HEADLEN ($r = -0.26$) and HWJ and INTORB ($r = 0.23$) are low, implying that in each case both variables are making strong, independent contributions to overall discrimination.

Discussion

The two primary goals of this study are to quantify size-related scaling patterns within and among species of *Nyctibatrachus* and to use these patterns as a framework in which to judge the validity of *Nannobatrachus* as a distinct genus.

The issue of generic recognition is always prob-

TABLE 3. Total canonical structure coefficients (table entries are the correlation of each residual variable).

Measure- ment	CV-1	CV-2
RHWJ	-0.47	0.64
RINTORB	0.24	0.69
RINTNAS	0.86	0.32
RHEADLEN	-0.69	0.39
RFEMUR	-0.09	0.40
RTIBIA	-0.23	0.40
RHINDFOOT	-0.15	0.01
RFORELIMB	-0.43	0.16

lematic (Mayr, 1942; Inger, 1958). In the case of these frogs, where diversification has proceeded largely via size shifts, I use the general approach outlined by Sweet (1980) and Potter and Sweet (1981). In their examination of cave-adapted hemidactyliine plethodontid salamanders, these authors outlined general patterns of morphological change associated with increasing cave adaptations in *Eurycea*. They then asked whether *Typhlomolge* was simply an extreme endpoint of this trend, or demonstrated qualitatively different patterns to reach the same endpoint. Having found the latter, they argued in favor of separate generic status for *Typhlomolge*, since it apparently represents a separate, monophyletic invasion of the cave environment.

I similarly use bivariate and multivariate scaling analyses to examine the fit of *Nannobatrachus* to the general size-scaling patterns found in *Nyctibatrachus*. The two genera are clearly very closely related, and in a previous survey, we failed to find diagnostic characters separating the two (Inger et al., 1984). If only size-related scaling of the kind found within *Nyctibatrachus* distinguishes it from *Nannobatrachus*, then the two are best considered congeneric. However, if *Nannobatrachus* shows evidence of reducing size via a different (presumably independent) pathway, then generic status may be appropriate.

Scaling patterns within and among species of *Nyctibatrachus* are generally very linear and consistent for the eight morphometric variables examined. This is obvious from visual inspection of Figure 1. Most individuals fall along the regression lines fit to *N. aliciae*, *N. major*, and *N. minor*, which are themselves indistinguishable from similar lines fit to *N. major* alone. There is very high overlap between adult *N. minor* and juvenile *N. major* of the same size, and in all cases there is virtually complete overlap between adult *N. aliciae* and *N. major* of similar size (fig. 1). From these analyses it appears that the general pattern of morphological evolution within this genus is for species to essentially stop growing with relatively juvenile morphologies at small sizes. This paedomorphic pattern could be accomplished either via progenesis or neoteny (Gould, 1977; Alberch et al., 1979), and they cannot be distinguished easily at present. However, the progenetic mechanism predicts a pattern of reduced ossification that can be examined in the future, using cleared and stained material.

The greatest apparent exception to this pattern is the difference between *N. humayuni* and large

N. major. However, this disparity must be viewed cautiously. The specimens of *N. humayuni* were collected from the vicinity of Bombay and preserved more than 30 years ago (Bhaduri & Kripalani, 1955). The potential artifacts imposed by these differences in age of specimens and state of preservation may be confounded with real differences between *N. humayuni* and *N. major*. The morphometric differences documented here, combined with other discrete characters, indicate that these are two distinct species. (*Nyctibatrachus humayuni* has a very blunt snout, very large, expanded fingertips and toe tips, and nearly completely webbed feet; *N. major* has a pointed snout, virtually no expansion of fingertips, slightly expanded toe tips, and feet about one-half webbed; also see Bhaduri & Kripalani, 1955.) However, the extent to which *N. humayuni* represents a radical shift from the scaling patterns found in the rest of the genus, especially in INTORB and INTNAS, should be confirmed with fresh material.

Is *Nannobatrachus* Valid?

The analyses presented here argue strongly against the recognition of *Nannobatrachus* as a genus distinct from *Nyctibatrachus*. In general, the fit of *Na. beddomi* to the scaling patterns found in *Nyctibatrachus* is very good (figs. 1–2; table 1). This is especially clear when making direct comparisons of *Na. beddomi* with *N. minor* of similar size. There may be slight size-specific differences between them in HEADLEN and HWJ, and there is clear differentiation in INTNAS. However, the general patterns are very similar.

The strongest argument for similar scaling relationships of *Na. beddomi* and *Nyctibatrachus*, however, comes from the discriminant function analysis. While overlap is not complete between *N. minor* and *Na. beddomi*, it is high, and overall, multivariate discrimination is no greater for *Na. beddomi* than for the species of *Nyctibatrachus* (fig. 2). Given the generally high levels of correct classifications in other studies of morphometrically similar species (e.g., Klecka, 1980; Shaffer, 1983, 1984), the misclassification level between *N. minor* and *Na. beddomi* further suggests high overlap. The Mahalanobis distance (a generalized euclidean distance) between the centroids of *Na. beddomi* and *N. minor* of 1.94 is the second smallest of the entire pairwise matrix; only the distance between *N. minor* and *N. aliciae* is marginally less (1.86). Thus, while some differentiation between

Na. beddomi and the others exists, *Na. beddomi* appears on morphometric criteria to be simply a diminutive species of *Nyctibatrachus*.

This interpretation is strengthened by additional information on the distributions of discrete characters. As discussed in Inger et al. (1984), pupil shape depends on state of preservation and is not a diagnostic character at the species or generic level; in life all species have diamond-shaped contracted pupils (see also Rao, 1937; Pillai, 1978). Unwebbed feet is also not diagnostic of *Nannobatrachus*, since *N. minor* lacks webbing. Variation in pigmentation of ova and presence of femoral glands diagnose various species of *Nyctibatrachus* but not *Na. beddomi* (see Inger et al., 1984, table 1, for the distribution of these characters). Only the absence of skin folds is unique to *Na. beddomi*, and this is best interpreted as a primitive lack of the derived condition found in the other species.

Clarke (1983) summarizes the osteological information available for *Nannophrys*, *Nannobatrachus*, and *Nyctibatrachus*. After discounting body size and foot webbing, three characters discussed by Clarke may separate *Na. beddomi* from the remaining species: the depth of the groove separating the outer metatarsals, the degree of separation of the nasals, and the shape of the distal end of the anterior ramus of the pterygoid. If all these characters consistently distinguish *Nyctibatrachus* from *Na. beddomi* (Clarke did not have *N. aliciae* or *N. minor* available), they could support the retention of *Nannobatrachus*. However, the morphometric evidence now available suggests strongly that *Na. beddomi* is a diminutive member of the *Nyctibatrachus* lineage and should be allocated to that genus.

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